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Habitat-correlated variation in blackbrush (*Coleogyne ramosissima*: Rosaceae) seed germination response

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Abstract

Blackbrush is a dominant shrub species in the transition zone between North American warm and cold deserts. Its seeds are dormant at dispersal and lose dormancy in response to moist chilling. Seeds from warmer low-elevation habitats have shorter chilling requirements and a higher optimum chilling temperature than those from colder habitats where winter snow regularly occurs. This ecotypic variation functions to time germination optimally in habitats with contrasting chilling regimes. Regulation of germination phenology is an important feature of the life history of this ecotonal species, which must be able to migrate elevationally through recruitment from seed in response to long-term climatic shifts in order to survive. Published by Elsevier Ltd.

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1. Introduction

The regulation of seed germination timing is a vital component of successful seedling establishment. It evolves in concert with other life history traits in response to selection regimes characteristic of particular habitats, particularly climatic regimes (Meyer et al., 1989, 1998; Meyer and Monsen, 1991). For desert shrubs, long life

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span coupled with relatively infrequent recruitment episodes is the norm (Bowers et al., 1995). In spite of their extended life spans, most desert shrubs rely exclusively on seedling recruitment for population persistence over the long term. Selection for germination timing mechanisms that optimize survival during occasional windows of opportunity in specific habitats should therefore be strong. This is especially the case for ecotonal desert shrub species, which rely on recruitment not just for in situ population persistence but also as a means of migrating in response to shifting climatic regimes. In this study, we examine variation in germination timing mechanism and its relationship with habitat in the ecotonal desert shrub blackbrush (*Coleogyne ramosissima* Torr.).

Blackbrush is a landscape dominant on over three million hectares in the southwestern United States, where it occupies a transition zone between the hot southern Mojave and Sonoran Deserts and the cold northern deserts or steppes of the Great Basin and the Colorado Plateau (Bowns and West, 1976; Benson and Darrow, 1981). Plant species diversity in blackbrush communities is commonly low. Blackbrush typically forms almost pure stands, especially on the unproductive, shallow soils where it is most abundant (Bowns and West, 1976; Jeffries and Klopatek, 1987). It is found at elevations of approximately 900–1900 m, between creosote bush (*Larrea tridentata*) or mixed desert shrub communities at lower elevations and juniper-sagebrush (*Juniperus-Artemisia*) communities at higher elevations (Wallace and Romney, 1972; Beatley, 1974; Bowns and West, 1976). Although important in terms of areal extent alone, blackbrush has been the subject of relatively few studies (Bowns and West, 1976; Jeffries and Klopatek, 1987; Lei, 1997). Many questions regarding seed production, recruitment, and establishment remain unanswered.

This study represents the first phase of a long-term research effort aimed at understanding the life history and regeneration biology of blackbrush in relation to its past and present geographic distribution (Pendleton et al., 1995). The elevational and latitudinal range that it occupies can be thought of as an ecotone between warm and cold deserts, a band that has undoubtedly shown vertical displacement or northward and southward shifts in response to climatic changes in the past (Cole and Webb, 1985; Hunter and McAuliffe, 1994). By clarifying how blackbrush responds to climatic regime in terms of regeneration in different parts of its range, we can infer both how it has responded in the past to achieve its current geographic distribution and how it is likely to respond to future climatic shifts.

Reproduction and recruitment in blackbrush are episodic. Occasional mast seed crops, produced when environmental conditions and plant resource status are favorable, are followed by several years of minimal seed output (Pendleton et al., 1995). Flowering occurs during April and early May in response to winter precipitation. Achenes ripen in June through early July (Beatley, 1974; Pendleton and Pendleton, 1998). Following dispersal, achenes are harvested and cached by heteromyid rodents in superficial scatterhoards. Environmental cues that trigger germination of these cached achenes have received little attention. The limited information available is based on seeds collected from populations of limited geographic range and stored for varying lengths of time prior to testing (Wallace and

Romney, 1972; Bowns and West, 1976; Lei, 1997). The common assumption that blackbrush is a paleoendemic species lacking in genetic variation, as originally postulated by Stebbins and Major (1965), has led researchers to extrapolate data from these few studies to all populations. As a result, the possibility of among-population variation in germination response has been overlooked.

The objectives of this study were: (1) to examine the germination characteristics of seeds collected from a large number of populations across the geographic and elevational range of blackbrush, (2) to explore the relationships between observed variation in blackbrush germination response and climate at the site of seed origin, and (3) to examine differences in the germination characteristics of blackbrush seeds produced in two different mast years.

2. Methods

Seeds (actually one-seeded achenes) were collected from 26 blackbrush populations in Utah and Nevada during June and July of 1991 by beating ripe achenes into a hopper (Table 1). Additional seeds were collected from five of these populations, plus one additional population, in June of 1997. Populations were chosen to represent the full geographic and elevational range of the species. Collections were cleaned using a series of screens to remove debris. Achenes retained within the calyx were removed using a rubbing board prior to screening. Only intact, mature achenes were used in the experiments. Achenes were generally free of insect damage. Cleaned collections were stored in unsealed manila envelopes under laboratory conditions (19–22°C, 30–40% relative humidity). All experiments were initiated within 8 weeks of harvest.

In order to learn whether blackbrush seeds exhibit conditional or temperature-dependent dormancy that is overcome by chilling, we incubated the seeds at a range of temperatures both without chilling and following chilling of increasing duration. Experiments included the following treatments: moist chilling at 2°C for 0, 2, 4, or 6 weeks, followed by incubation for 4 weeks at 12-h alternating temperatures of 5/15°C, 10/20°C, 15/25°C, or 20/30°C. All 26 1991 collections were incubated at 10/20°C following chilling at 2°C for 0, 2, 4, or 6 weeks, while a subset of ten populations representative of the sampled elevational and geographic range was included in the complete chilling by incubation temperature factorial experiment. The six 1997 collections were also subjected to the complete factorial design.

Germination rate at near-freezing temperature was estimated from time course data obtained by placing seeds at 2°C for 15 weeks and counting germinated seeds on a weekly basis. Germination rate at 5/15°C was also estimated from time course data obtained for the ten 1991 collections included in the full factorial design by leaving the seeds in 5/15°C incubation for a total of 10 weeks and counting germinated seeds at weekly intervals.

For each treatment, four replications of 25 seeds were counted out from each seed collection. The seeds were placed between two moistened blue germination blotters (Anchor Paper, St. Paul MN) in 100-mm plastic Petri dishes. The dishes were

Table 1

Locations and years for blackbrush seed collections. Within each geographic group, locations are ranked by elevation

Population	State	Elevation (m)	Latitude/longitude	Year of collection
Mojave group				
Hurricane	UT	976	37°09′N/113°17′W	1991
Legrande Heights	UT	976	37°09′N/113°18′W	1991
Toquerville road	UT	1128	37°15′N/113°16′W	1991, 1997
Toquerville exit	UT	1159	37°16′N/113°17′W	1991
Hurricane Mesa	UT	1170	37°08′N/113°16′W	1991
Winchester Hills	UT	1189	37°13′N/113°37′W	1991, 1997
Red Rocks Overlook	NV	1189	36°09′N/115°25′W	1991
Snow's Canyon Rim	UT	1235	37°14′N/113°37′W	1991
Browse turnoff	UT	1259	37°21′N/113°16′W	1991, 1997
Kyle Canyon	NV	1280	36°17′N/115°25′W	1991
Potosi Pass road	NV	1372	36°00′N/115°32′W	1991
Veyo road	UT	1402	37°16′N/113°38′W	1991
Beaver Dam summit	UT	1450	37°05′N/113°51′W	1997
Lee Canyon	NV	1585	36°24′N/115°32′W	1991
Colorado Plateau group				
Hite turnoff	UT	1280	37°48′N/110°18′W	1991
Mexican Hat	UT	1304	37°09′N/109°50′W	1991
Gemini Bridges Turnoff	UT	1341	38°34′N/109°35′W	1991
North of Hanksville	UT	1356	38°47′N/110°27′W	1991
South of Bluff	UT	1402	37°15′N/109°44′W	1991
Bridges road mile Marker 57	UT	1402	37°45′N/110°16′W	1991
Arches National Park	UT	1463	38°43′N/109°32′W	1991, 1997
Dirty Devil turnoff	UT	1494	38°38′N/110°36′W	1991, 1997
White Mesa	UT	1524	37°30′N/109°29′W	1991
Bridges road mile marker 68	UT	1524	37°40′N/110°13′W	1991
Needles-Canyonlands	UT	1535	38°08′N/109°46′W	1991
Little Rockies	UT	1646	37°47′N/110°39′W	1991
Island in the Sky	UT	1866	38°35′N/109°47′W	1991

randomized in stacks and incubated in the dark, but exposed to light during reading. Tap water was added to the blotters as needed to maintain moisture during the experiment. Germinated seeds were counted and removed from the dishes 1–2 times per week. Seeds were considered germinated if the radicle extended 5 mm or exhibited bending. At the end of each experiment, viability of ungerminated seeds in each dish was determined using cut test procedures (Association of Official Seed Analysts, 1988). Seeds that were filled with an intact, white, firm embryo were scored as viable.

Germination values were expressed as percentage of viable seeds in each replicate dish; viability was generally high (88% overall). Percentage data were arcsine-transformed and analysed using analysis of variance (ANOVA) or general linear model (GLM) procedures (SAS Version 6 for PC; SAS Institute Inc., 1990).

The factorial experiments for 1991 and 1997 were analysed using three-way fixed effects ANOVA. To obtain treatment means separations within populations, we used a Tukey test with the error mean squares from above ANOVA's as the error terms (Quinn and Keough, 2002).

The chilling data for 26 1991 collections incubated at $10/20°C$ were analysed using analysis of covariance (ANCOVA). Because of a lack of climatic data, elevation was considered a surrogate for winter climate in the analysis, where it was used as the continuous variable. Geographic group (Mojave or Colorado Plateau) and chilling duration were the class variables.

Means separations for chilling treatments within populations for the 26 collections at $10/20°C$ were obtained via the Tukey test. The error term used for these means separations was the error mean square from a fixed effects ANOVA on the whole data set with population and chilling treatment as main effects (Quinn and Keough, 2002).

ANCOVA's with collection site elevation as the continuous variable were performed on 1991 data from the $5/15°C$ incubation temperature treatment (ten populations). In the first ANCOVA, chilling treatment (no chilling versus a 2-week chill) was the class variable, while germination percentage after 4 weeks of incubation was the response variable. In a second ANCOVA, chilling regime ($2°C$ versus $5/15°C$) was the class variable, while germination percentage after 10 weeks of incubation was the response variable. Geographic group was not used as a class variable in these two analyses because geographic group membership and elevation were confounded for the ten populations included. The three lowest elevation populations were in the Mojave group, while the remaining seven were in the Colorado Plateau group.

We also performed ANCOVA on the $2°C$ continuous chilling data for 26, 1991 collections, again with elevation as the continuous variable and geographic group as the class variable. The response variable was mean germination rate, the reciprocal of days to 50% of total germination; all viable seeds germinated. Values for days to 50% were derived using linear interpolation from the 15-week germination time course data for each seed population and replication.

3. Results

Blackbrush seeds from both 1991 and 1997 mast years were largely dormant without chilling (Fig. 1). There was a highly significant interaction between incubation temperature and chilling duration each year (Table 2). At the optimum (lowest) temperature of $5/15°C$, a sizeable fraction could germinate even without chilling, while there was little or no germination at higher temperatures (Fig. 1). With each 2-week increment in chilling duration, there was an increase in the germinable fraction at each incubation temperature. The size of this increase was smaller at first at the higher incubation temperatures and larger at the lower temperatures. After 6 weeks of chilling, germination percentage averaged near 90% overall and the differences between incubation temperatures had largely
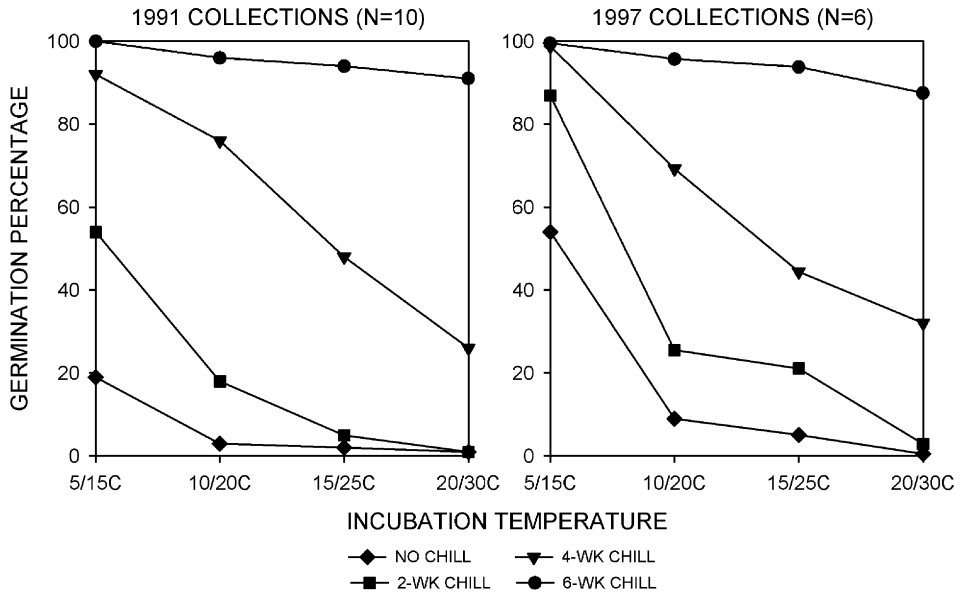
Fig. 1. The interaction between moist chilling treatment (0–6 weeks at 2°C) and post-chilling incubation temperature for 10, 1991 and for six, 1997 blackbrush seed collections.

disappeared. Chilling at 2°C thus expands the range of temperatures over which germination can occur upward to include summer temperatures, as well as quickly removing dormancy at more optimal lower temperatures characteristic of spring.

Populations differed in both their overall mean germination percentages (population main effect) and in their response to incubation temperature and chilling duration (population interactions) in both 1991 and 1997 (Table 2). These differences are evident when the responses of individual seed collections are compared (Tables 3 and 4).

The pattern of dormancy loss as a function of chilling duration and incubation temperature was similar for 1991 and 1997 collections, but there were some differences in detail, especially for the shorter chilling durations (Fig. 1). The 1997 collections were considerably less dormant without chilling, with over twice the germination at 5/15°C and with some germination even at 15/25°C. They also tended to be more responsive to a 2-week chill than 1991 collections. It is not possible to compare these two sets of data formally, because there is little overlap in the populations included (Tables 3 and 4). But the same pattern emerges when populations common to the two data sets are compared. Both the Toquerville Exit and Arches populations showed considerably higher germination percentages in 1997 than in 1991.

When seeds of 26 populations were incubated at 10/20°C, their response to prior chilling varied as a function of both collection site elevation and geographic origin (Tables 2 and 5, Fig. 2). The ANCOVA accounted for 90% of the observed

Table 2
ANCOVA results for the chilling experiment with 26 blackbrush collections in 1991, and ANOVA results for chilling × incubation factorial experiments with 10 blackbrush collections in 1991 and six blackbrush collections in 1997

Effect	DF (effect, error)	*F*-value	Probability
Chilling experiment 1991			
Chilling treatment (class variable)	3400	23.33	0.0001
Geographic group (class variable)	1400	3.23	n.s.
Elevation (continuous variable)	1400	26.84	0.0001
Chilling treatment × geographic group	3400	3.23	0.0224
Chilling treatment × elevation	3400	3.59	0.0139
Geographic group × elevation	1400	0.82	n.s.
Geographic group × elevation × chilling treatment	3400	2.35	0.071
Chilling × incubation temperature factorial 1991			
Population	9480	11.02	0.0001
Chilling treatment	3480	2897.38	0.0001
Incubation temperature	3480	532.89	0.0001
Population × chilling treatment	27,480	4.10	0.0001
Population × incubation temperature	27,480	2.74	0.0001
Chilling treatment × incubation temperature	9480	41.00	0.0001
Population × chilling treatment × inc. temperature	81,480	1.12	n.s.
Chilling × incubation temperature factorial 1997			
Population	5288	18.51	0.0001
Chilling treatment	3288	1420.91	0.0001
Incubation temperature	3288	741.71	0.0001
Population × chilling treatment	15,288	7.52	0.0001
Population × incubation temperature	15,288	6.32	0.0001
Chilling treatment × incubation temperature	9288	41.69	0.0001
Population × chilling treatment × inc. temperature	45,288	2.54	0.0001

Arcsine-transformed germination percentage after 4 weeks at the post-chilling temperature regime was the response variable.

experimental variation overall. As in the factorial experiments, germination percentage increased with chilling duration (chilling treatment main effect). Response to chilling decreased with increasing elevation, i.e., the slope of the elevation–germination percentage relationship was significantly negative overall (elevation main effect).

There was also a significant interaction between elevation and chilling duration in this experiment (Table 2, Fig. 2). Without chilling, there was little germination regardless of collection site elevation, and the slope of the relationship was near zero. The effect of elevation on germination response is seen most clearly in steeper negative slopes at intermediate chilling durations.

The significant interaction between geographic group and chilling duration is evident in the higher post-chilling germination percentages for Colorado Plateau collections, which run in controversion to their generally higher collection site elevations (Tables 2 and 5). The regression lines for the Colorado Plateau group lie

Table 3

Germination percentages after chilling 0–6 weeks at 2°C followed by 4-week incubation at 5/15°C, 10/20°C, 15/25°C, or 20/30°C for 1991 blackbrush seed collections[a]

Population	Incubation temperature															
	5/15°C				10/20°C				15/25°C				20/30°C			
	Weeks of chilling				Weeks of chilling				Weeks of chilling				Weeks of chilling			
	0	2	4	6	0	2	4	6	0	2	4	6	0	2	4	6
Mojave Group																
Legrande Heights	25e	78b	98a	100a	7fg	27e	64c	93a	2fg	10f	49d	93a	0 g	2 fg	21e	74b
Toquerville Exit	24e	68c	88b	99a	5fg	21e	64c	97a	3fg	5fg	33d	94a	3fg	0 g	11f	87b
Hurricane Mesa	36e	76c	98a	100a	2hi	28f	84b	97a	1i	10h	45d	96a	0i	1i	19 g	93a
Colo. Plat. Group																
Hite Turnoff	28e	60c	95ab	100a	2f	22e	90b	95ab	4f	3f	48d	93ab	0f	2f	30e	95ab
Mexican Hat	19e	59c	92ab	100a	0f	24e	86b	96ab	2f	9f	57c	95a	0f	5f	41d	95a
Arches NP	7f	41d	90b	100a	0f	8f	71c	94ab	1f	1f	49d	97ab	0f	0f	31e	94ab
White Mesa	11d	37c	91b	100a	2de	9d	75b	98ab	2de	5de	43c	92ab	0e	0e	41c	96ab
Needles	8ef	45d	87b	100a	2f	7ef	72c	94ab	1f	3f	44d	85b	0f	0f	12e	83b
Little Rockies	26e	48d	95ab	100a	4f	22e	89b	97ab	1f	4f	74c	98a	0f	1f	29e	98a
Island in the Sky	4e	30d	84b	99a	2e	7e	65c	97a	0e	2e	35d	94a	0e	1e	25d	94a
Overall Mean	18.8	54.2	91.8	99.8	2.6	17.5	76.0	95.8	1.7	5.2	47.7	93.7	0.4	1.1	26.0	90.9

[a] Within a collection (row), means followed by the same lowercase letter are not significantly different at the $p < 0.05$ level according to a Tukey test using the error mean square from the overall ANOVA as the error term (Quinn and Keough, 2002).

consistently above those for the Mojave group for all but the no chilling treatment (Fig. 2).

The evidence for differences between the two geographic groups in the effect of collection site elevation (slope) is weak (Table 2, group × elevation interaction not significant), indicating that the slight differences between geographic groups in plotted slopes are generally not important (Fig. 2). There is a marginally significant three-way interaction, however (Table 2, geographic group × elevation × chilling treatment, $p < 0.10$). This is probably due to the fact that the slope for the Colorado Plateau group after a 6-week chill is essentially flat (i.e., all populations at or near 100%), while the slope for the Mojave group is still negative.

A significant negative relationship between collection site elevation and germination percentage was also observed for seeds incubated at the optimal temperature of 5/15°C (elevation main effect; Fig. 3A). Once again, chilling significantly increased germination percentage overall (chilling treatment main effect). The chilling by elevation interaction was marginally significant, with lower elevation collections tending to be more responsive to a 2-week chill than higher elevation collections, a result similar to that obtained for seeds incubated at 10/20°C.

When the effect of incubation temperature (2°C vs. 5/15°C) was included along with collection site elevation in ANCOVA, seeds germinated to higher percentages

Table 4
Germination percentages after chilling 0–6 weeks at 2°C followed by 4-week incubation at 5/15°C, 10/20°C, 15/25°C, or 20/30°C for 1997 blackbrush seed collections[a]

| Population	Incubation temperature															
	5/15°C				10/20°C				15/25°C				20/30°C			
	Weeks of chilling				Weeks of chilling				Weeks of chilling				Weeks of chilling			
	0	2	4	6	0	2	4	6	0	2	4	6	0	2	4	6
Mojave group																
Toquerville Exit	84b	98a	100a	100a	19e	48c	84b	99a	9f	37d	39d	95ab	0 g	0 g	26e	93a
Winchester Hills	53d	86b	97a	99a	11f	20e	67c	89b	5fg	7fg	47d	83b	1 g	2 g	9fg	72c
Browse Exit	58c	86b	100a	100a	7fg	14f	50c	95a	0 g	6fg	39d	97a	0 g	2 g	28e	82b
Beaver Dam Summit	64c	87b	100a	99a	11f	29d	82b	95ab	9fg	36d	36d	94ab	2 g	2 g	20e	90b
Colo.Plat. Group																
Arches Nat. Park	31f	80b	99a	99a	1h	10g	66c	99a	3gh	6gh	54d	98a	0h	1h	42e	93a
Dirty Devil Turnoff	34e	85b	97a	100a	4fg	31e	66c	99a	3ef	34e	51d	97a	0g	10f	67c	96a
Overall Mean	54	87	99	100	9	26	69	96	5	21	44	94	1	3	32	88
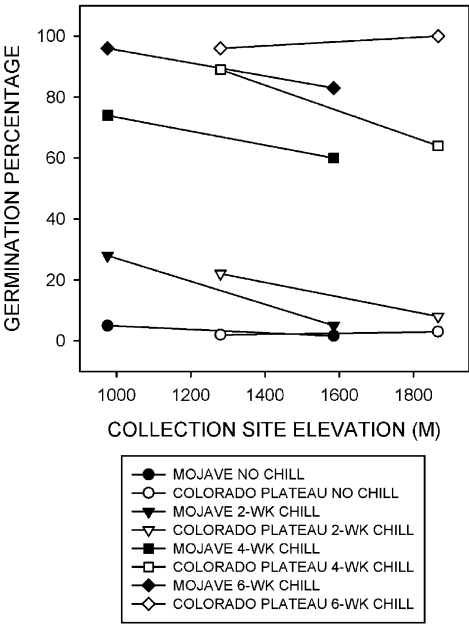
Fig. 2. The effect of chilling treatment, geographic group, and collection site elevation on germination percentage of seed collections from 26 blackbrush populations after 4 weeks at 10/20°C in response to 0–6 weeks of chilling at 2°C. Plotted lines are from regressions by geographic group and chilling duration.

Table 5
Germination percentages after chilling periods of 0–6 weeks at 2°C followed by incubation at 10/20°C for 4 weeks for 26 blackbrush seed collections made in 1991[a]

Population	Chilling duration (weeks)			
	0	2	4	6
Mojave group				
Hurricane	2d	33c	79b	93a
Legrande Heights	7d	27c	64b	93a
Toquerville road	5d	20c	78b	90a
Toquerville Exit	5d	21c	64b	97a
Hurricane Mesa	2d	28c	84b	97a
Winchester Hills	3d	13c	59b	94
Red Rocks Overlook	4d	33c	87b	96a
Snow's Canyon Rim	2c	4c	59b	93a
Browse turnoff	0c	6c	56b	91a
Kyle Canyon	5d	29c	95a	85b
Potosi Pass road	2c	5c	45b	73a
Veyo road	1c	6c	43b	88
Lee Canyon	3d	11c	71b	84a
Group Mean	3.0	18.2	68.0	90.3
Colorado Plateau group				
Hite turnoff	2c	22b	90a	95a
Mexican Hat	0d	24c	86b	96a
Gemini Bridges turnoff	0c	18b	90a	95a
North of Hanksville	8c	36b	100a	100a
South of Bluff	1d	11c	85b	99a
Bridges road MM57	0d	8c	76b	95a
Arches National Park	0d	8c	71b	94a
Dirty Devil turnoff	7d	27c	91b	98a
White Mesa	2d	9c	75b	98a
Bridges road MM68	2d	25c	60b	85a
Needles-Canyonlands	2c	66b	72b	94a
Little Rockies	4d	22c	89b	97a
Island in the Sky	2c	7c	65b	97a
Group mean	2.3	21.8	80.8	95.6

[a] Within a collection (row), means followed by the same letter are not significantly different at the $p < 0.05$ level according to a Tukey test using the error mean square from ANOVA that included population and chilling treatment as main effects (Quinn and Keough, 2002).

overall after 10 weeks at 2°C than at 5/15°C (incubation temperature main effect; Fig. 3B). The overall effect of elevation was nil, but there was a strong incubation temperature by elevation interaction. Germination percentage at 10 weeks increased with elevation when seeds were incubated at 2°C, while when they were incubated at 5/15°C the opposite effect was seen. This suggests that the effectiveness of 5/15°C as a chilling regime decreased with increasing collection site elevation. Low elevation collections were able to respond to this marginal chilling regime, while high elevation
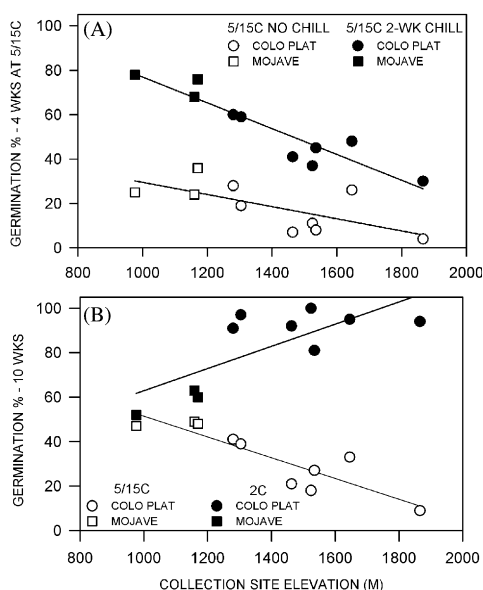
Fig. 3. (A) The effect of collection site elevation and chilling treatment on germination percentage for 10 blackbrush seed collections after 4 weeks at 5/15°C without chilling and after 2 weeks of moist chilling at 2°C (ANCOVA results: elevation main effect, $F = 56.12$, df. $= 1, 76$, $p < 0.0001$; chilling treatment main effect $F = 14.12$, df. $= 1, 76$, $p < 0.0003$; elevation × chilling treatment interaction, $F = 2.74$, df. $= 1, 76$, $p < 0.1018$). (B) The effect of collection site elevation and incubation temperature on germination percentage after 10 weeks of incubation at 5/15°C and at 2°C. (ANCOVA results: elevation main effect $F = 0.14$, df. $= 1, 76$, n.s.; incubation temperature main effect, $F = 23.94$, df. $= 1, 76$, $p < 0.0001$; elevation × incubation temperature interaction, $F = 57.82$, df. $= 1, 76$, $p < 0.0001$). Geographic group identity indicated on graphs but not included in analysis.

collections were not. In contrast, high elevation collections germinated to higher percentages than low elevation collections during 10 weeks at 2°C. This indicates that low elevation collections were less able to respond quickly to the near-freezing temperature regime, probably because they require a higher temperature for optimum chilling.

The effect of geographic group and elevation on germination during chilling at 2°C is seen for the larger 1991 data set as well (Fig. 4). Colorado Plateau collections germinated faster overall at 2°C than Mojave collections, as demonstrated by the higher regression line and the general lack of overlapping points (geographic group main effect). The elevation main effect was not significant in this analysis, but the elevation by geographic group interaction was significant. A much tighter relationship and a more positive slope was observed for the Mojave group than for the Colorado Plateau group, whose germination rate values are scattered almost at random and whose slope is essentially flat. These results generally confirm the idea that seeds of populations from higher, colder sites have a lower optimum temperature for chilling and can thus germinate faster at near-freezing temperatures
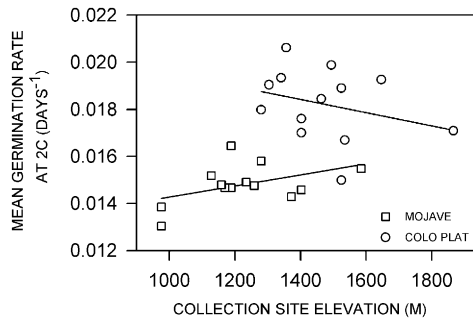
Fig. 4. The effect of collection site elevation and geographic group on mean germination rate during 15 weeks of moist chilling at 2°C for 26 blackbrush seed collections. (ANCOVA results: elevation main effect, $F = 0.88$, df. $= 1, 100$, n.s.; geographic group main effect $F = 12.31$, df. $= 1, 100$, $p < 0.0007$; elevation $\times$ geographic group interaction, $F = 5.12$, df. $= 1, 100$, $p < 0.0258$).

than seeds from lower elevation sites, where sustained chilling temperatures are likely to be higher. The effect of geographic group was probably due to the fact that winters on the Colorado Plateau are colder but drier than winters at comparable elevations in the Mojave Desert.

4. Discussion

The experiments reported here clearly demonstrate the existence of habitat-correlated variation in seed germination response for blackbrush. In some ways the patterns we observed are in accordance with patterns observed for other species that range from the warm deserts up to higher elevations. Within a species or group of closely related species, populations from the warm desert commonly have lower primary seed dormancy and shorter chilling requirements than populations from higher elevations, the pattern that was observed for blackbrush in this study (e.g., Meyer, 1992; Meyer and Kitchen, 1994; Meyer et al., 1998). This variation in chilling response is probably a result of evolutionary fine tuning of chilling response to variation in local chilling regimes.

Lower-elevation blackbrush populations rarely encounter sustained chilling at the near-freezing temperatures found beneath snow cover. They are adapted to respond to the warmer and more fluctuating chilling regimes characteristic of habitats where winter precipitation falls in the form of rain. This explanation is supported by the faster and more complete germination of seeds from low elevation populations under the 5/15°C temperature regime. In contrast, the populations from higher, colder sites are better adapted for chilling at near-freezing temperature. They must be able to respond relatively quickly under these conditions, because of the ephemeral nature of snow cover on these sites. This is reflected in their faster germination in the 2°C continuous chilling regime. The colder, drier winters on the Colorado Plateau appear to have selected for blackbrush seeds that can respond more quickly to chilling at

near-freezing temperatures than seeds from comparable elevations in the Mojave Desert.

Much but not all of the variation in germination response in these experiments could be explained in terms of collection site elevation and geographic origin of the seeds. The difference between years in dormancy status at particular sites suggests that there is considerable plasticity in germination patterns, perhaps in response to environmental conditions during ripening. This plasticity may account for some of the discrepancies between germination values predicted by elevation and geographic group and observed responses of particular seedlots, i.e., the scatter around the predicted regression lines. Another likely explanation is that collection site elevation is an imperfect index of winter climate even within a geographic region.

As mentioned earlier, blackbrush is a transitional species that occupies a boundary that has shifted in recent geologic time. Analysis of packrat middens suggests a 50–100-m downward movement of the blackbrush zone along elevational gradients in the Mojave (Cole and Webb, 1985; Hunter and McAuliffe, 1994). The timing of this appearance of blackbrush at lower elevation sites (1050–1795 AD) was coincident with the Little Ice Age, a time when the climate was cooler and wetter than present. Movement of the blackbrush zone along an elevational gradient is entirely dependent upon successful seedling establishment.

Mature blackbrush plants are physiologically well adapted to persist under less than optimal conditions. Individual plants are long-lived and may have lifespans of 400 years (Christensen and Brown, 1963). The estimated mortality rate is approximately 4% in 100 years (Robert Webb, personal communication). Long-term water use efficiency of adult plants, as measured through carbon isotope discrimination, is extremely high (Sandquist et al., 1993) and, in contrast with other desert shrubs such as *Atriplex canescens* and *Artemisia filifolia*, blackbrush can efficiently utilize summer rainfall events (Lin et al., 1996; Gebauer and Ehleringer, 2000). Furthermore, our observations indicate that plants are capable of remaining dormant, with no new leader growth or leaf production, during times of extended (>3 year) drought. These traits allow established populations of blackbrush to persist for long periods of time, even after changes in environmental conditions preclude seedling establishment.

We concur with Stebbins and Major (1965) that blackbrush, which belongs to a monotypic genus that is taxonomically isolated in the Rosaceae, is a probably a paleoendemic, but the idea that it possesses little genetic variation must be rejected. Schuster et al. (1994) reported high levels of genetic (isozyme) variation in four desert shrub species, including *Coleogyne ramosissima*. Although we cannot demonstrate conclusively that the variation in germination response we detected was genetically based, work with the genetics of seed dormancy in the related species *Purshia tridentata* (Meyer and Pendleton, 2000) strongly suggests that such variation represents ecotypic differentiation.

Additional work is needed to confirm that the habitat-correlated differences in blackbrush seed germination response that we observed have ecological relevance. We need to measure germination and emergence phenology and consequent establishment success for seeds from different populations in contrasting habitats.

If the scenario of shifting blackbrush elevational zones in response to climate change is generally correct, it should be possible to identify the leading edge of such a migration as well as its trailing edge by examining variation in age class structure and recruitment success across an elevational gradient within the blackbrush zone.

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